

Biodiversity of Wasp Species (Insecta: Hymenoptera) in Burned and Unburned Habitats of Yellowstone National Park, Wyoming, USA

JEFFREY A. LOCKWOOD, SCOTT R. SHAW, AND JANE M. STRUTTMANN

Department of Plant, Soil, and Insect Sciences, University of Wyoming, Laramie, Wyoming
82071-3354, U.S.A.

Abstract.—Four months of Malaise trapping in two burned and unburned habitats, 2 yr after the 1988 fires in Yellowstone National Park (YNP), resulted in a total of 603 species from 36 families of Hymenoptera. The majority of the species were Ichneumonoidea (60%). The unburned habitats peaked at 107 and 113 species during a 2-week sampling period, while the corresponding burned habitats had maxima of 88 and 90 species. Hymenopteran species diversity (Shannon-Wiener) was primarily a function of richness, with evenness differing only slightly between habitats (range 78–98%). Diversity and richness in burned sites were generally 75–85% of the values in unburned sites. The two burned habitats had greater community similarity ($23.5 \pm 4.6\%$) than that found between adjacent burned and unburned habitats at either site ($13.8 \pm 1.9\%$). The unburned habitats had relatively low community similarity ($12.4 \pm 5.4\%$), indicating a surprisingly high degree of between-patch endemism in mature lodgepole pine forests. This endemism also suggests the possibility that species may have been extirpated from some burned habitats in YNP. Comparison of trophic associations, including inference of relative (ordinal) host abundance from parasitoid abundance, indicate that burned habitats were dominated by herbivores of nonwoody plants and unburned habitats are characterized by fungivores and detritivores. These findings are consistent with observations that burned sites were typified by the establishment of grasses and forbs and the loss of litter, which would have been concomitant with a deceleration of arthropod- and fungal-mediated organic decomposition. There was no evidence of dead wood having provided a major source of nutrients for insects in burned habitats, and there was no evidence of insect outbreaks in the region of our trap sites.

INTRODUCTION

The 1988 fires in Yellowstone National Park (YNP), Wyoming, USA, burned 400,000 ha or 45% of the park (Christensen *et al.* 1989). Knight and Wallace (1989) predicted that overall species richness would gradually increase over a period of 25 yr, eventually surpassing that of the old growth forest prior to the fires. They also noted that some species (e.g., bark beetles) would likely outbreak shortly after the fire. The reliability of these forecasted dynamics is contingent upon the similarity of fires investigated in previous research (Taylor 1969, 1973, 1974; Taylor and Barmore 1980; Knight 1987) to those that occurred in 1988. Although some evidence

suggests that extremely large-scale fires have been part of the history of YNP (Christensen *et al.* 1989), catastrophic fires of the magnitude seen in 1988 have never been studied. In this context it is important to consider that striking qualitative changes in ecological conditions and processes may result from increasing (or decreasing) the scale of reference (Allen and Hoekstra 1992).

Before the 1988 fires, managers anticipated the development of a new biotic community immediately following a burn, with insects quickly utilizing the new food sources provided by the freshly killed trees (Despain 1978). Based on experience with smaller fires, it was posited that few vertebrates and no species, were lost in

the 1988 fires (Christensen *et al.* 1989, Schullery 1989, Skinner 1990). While some insect populations were undoubtedly reduced by the fires, there were several observations that suggested that insects were recovering within a year (McEaney [YNP Ornithologist] *in* Carr 1990, Skinner 1990, Varley [YNP Chief of Research] *in* Jeffery 1990), and anecdotal evidence indicated possible outbreaks of species capable of exploiting fire-damaged trees (Romme and Despain 1989, Skinner 1990). Qualitative observations indicated that the rate of recolonization for some taxa was extraordinarily rapid. Skinner (1990) reported finding black bears feeding on abundant, large wood wasps while they oviposited in the smoldering stumps, and Lewin (1988) forecasted a resurgence of insects exploiting the new growth of grasses and herbs. Such evidence was extended into a more general prediction that biodiversity was or would be enhanced by the fires (Knight and Wallace 1989, Romme and Despain 1989, Varley *in* Jeffery 1989, 1990). Conversely, Elfring (1989) and Conniff (1989) warned that reported recovery rates were overestimated (Elfring 1989, Conniff 1989).

The observations and predictions regarding the recovery of fire-adapted and other insect species form an important and compelling basis for developing and testing ecological hypotheses. However, the controversy surrounding competing claims of ecological recovery persists largely due to a lack of quantitative ecological data. Despite the intriguing observations of insect fauna, there are no published data related to the post-fire terrestrial insect fauna of YNP. There have only been about a dozen published studies of entomological research within the Park in the last 20 yr, and the only relevant, quantitative data were restricted to the litter habitat (Lavigne *et al.* 1990). Indeed, the insect fauna of YNP has been estimated to range from 12,000 to "tens of thousands" of species (Clark *et al.* 1989), the vast majority

(>95%) of which were not documented prior to the fires. As Minshall *et al.* (1989) noted, a more complete faunal database and systematic sampling are essential in assessing the impacts of the fires to the biodiversity of YNP (Christensen *et al.* 1989, Schullery 1989, Roemhild 1994). Simply put, without empirical data it is not possible to assess predictions of the rate and form of ecological recovery.

The central questions related to the short-term effects of the YNP fires on biodiversity are: 1) has species diversity, richness, or evenness increased in the time since the fires, 2) are any species found only in burned areas (suggesting the potential for enhanced richness or diversity) or unburned areas (suggesting the possibility of extirpation from YNP), and 3) have there been any insect outbreaks of fire-adapted species? Initial studies demonstrated that in the 2 yr following the fires insect species diversity in the litter habitat were almost invariably reduced in burned locations relative to unburned sites, although diversity consistently increased in burned sites from 1989 to 1990 (Lavigne *et al.* 1990). Because extrapolating from this habitat to the forest ecosystem is problematical, we undertook an intensive study of the Hymenoptera as an indicator taxon (*sensu* Cook 1976, Sheehan 1984, Munn 1988, Hawksworth and Ritchie 1993) in 1990.

The Hymenoptera were chosen as the indicator of biodiversity because: 1) they are easy and cost-effective to collect, 2) the parasitic species rely on a wide spectrum of herbivorous hosts, 3) the parasitoids of herbivorous insects provide an indirect but effective measure of biodiversity of this lower trophic level and the condition of the vegetative community, and 4) one of us (SRS) is a hymenopteran systematist, facilitating identification work [see Noss (1990), Spellerberg (1991), and Hawksworth and Ritchie (1993) for more complete descriptions of the desired qualities of a biodiversity indicator taxon]. Logisti-

cal, financial, and regulatory limitations restricted our study to a single year of intensive data collection, 2 yr after fires, so we adopted the strategy of comparing adjacent burned and unburned areas to address the effects of the fires and the nature of the recovery.

MATERIALS AND METHODS

Two sites in Yellowstone National Park were chosen for setting pairs of Townes-style Malaise traps (approximately $2 \times 2 \times 2$ m; Golden Owl Publishers, Lexington Park, MD). The number of sites and traps was limited by logistical and resource constraints and YNP policies regarding the frequency and intensity of trap monitoring. These sites represented different fires within YNP (which merged into the Snake River fire complex) and therefore functioned as true replicates. The northern sites included a burned habitat and an unburned (control) habitat, 5.4 and 5.8 km, respectively, from the South Entrance to the Park. The southern sites included a severely burned habitat and an unburned (control) habitat, 4.0 and 2.3 km from the South Entrance. Control habitats were selected to represent topographic and presumed vegetative characteristics of the burned areas prior to the fires. Malaise trapping is highly efficient but may be influenced by the local conditions, so trap positioning and microhabitat conditions were replicated as precisely as possible between sites. As such, physical proximity was secondary to the ecological characteristics.

The traps were in adjacent burned and unburned areas, about 500 m from the edge of the burn. Traps were first set during the last week of May, 1990. Owing to YNP regulations that traps be constantly "attended", they could only be left in place for 2-wk intervals. Insects were collected from the traps on June 10 and 14, July 7 and 14, August 11 and 19, and September 7. Traps were damaged by weather, wildlife, or vandals on five occasions,

resulting in missing data (northern burned site on July 7; southern unburned site on July 14; northern burned, northern unburned, and southern burned sites on September 7). The collections were stored in 70% ethanol and returned to the laboratory where the Hymenoptera were separated. The Hymenoptera were prepared, identified to subfamily (in some cases genus, and occasionally species), and sorted to morphospecies. Voucher specimens of all morphospecies are deposited in the Rocky Mountain Systematic Entomology Laboratory, University of Wyoming, Laramie.

We examined the hymenopteran community structure from the perspectives of diversity, evenness, and richness (Kotila 1986). As with all sampling methods, Malaise traps are biased in the groups that they collect (e.g., primarily small insects flying <2 m above ground level (Matthews and Matthews 1971, Darling and Packer 1988)). However, the application of diversity indices to selected portions of a biotic community (e.g., Kappelle et al. 1995) is appropriate as long as the results are interpreted in the context of the constraints of the sampling methodology (Southwood 1978).

Diversity (a measure of both the abundance and equitability of species) was expressed using the Shannon-Wiener index (H) (Southwood 1978). This measure was chosen because: 1) it is normally distributed (Taylor 1978), 2) it is more appropriate than the Simpson-Yule index, which is strongly influenced by the underlying distribution for samples with more than 10 species (May 1975), 3) it was more appropriate than the Berger-Parker index because there were several cases of co-dominant species, 4) it is dependent on both evenness and richness (Magurran 1988), and 5) it is perhaps the most commonly encountered index in the literature (Magurran 1988, Spellerberg 1992) and was used in the analysis of litter arthropod communities after the YNP fires (Lavigne

et al. 1990). The disadvantages of using H are that the index is a purely relative measure, without absolute meaning [as opposed to the Simpson-Yule index (Southwood 1978)], but we were particularly interested in comparisons between communities from burned and unburned habitats, so the relativity of this index was not problematical. In addition, H is not sensitive to the character of the ratio of species to individuals and it is dominated by the abundant species (May 1975), but these qualities did not constitute disadvantages in the context of our application.

Having chosen H as the measure of diversity, we used the Shannon-Wiener index of evenness (Kotila 1986). This measure is the ratio of the maximum value of H (assuming that the individuals were evenly distributed among the species) to the realized value of H . As such, this measure of evenness ranges from 0.0 to 1.0.

We expressed the species richness as the number of species. Although this measure has the clear advantage of simplicity, it has the disadvantage of oversensitivity to numerically rare species. Findley (1973) and Hendrickson and Ehrlich (1971) have criticized restricting expressions of diversity to the number of species present while failing to consider the forms and functions of the species. However, our assessment of species richness avoids this pitfall in that we employed concomitant analyses of diversity and we have a good understanding of the ecological functions of the species in the taxon of interest. Given the sampling constraints, the use of numerical species richness is appropriate (Magurran 1988).

We used analysis of variance (MSU-STAT software, version 3.2) to assess differences in the ecological measures (diversity, evenness, richness) between burned and unburned habitats; an arc sine transformation was applied to evenness (Snedecor and Cochran 1980). Measures from the sites representing each habitat type (burned and unburned) were pooled into

three time blocks: spring (before 21 June, $N = 4$), early summer (between 21 June and 1 August, $N = 3$) and late summer (after 1 August, $N = 4$), so as to allow an equal number of data points in each block and eliminate the confounding effects of phenology.

To assess the taxonomic overlap between habitats and sites (i.e., community similarity), we used a direct calculation of percent similarity (Kotila 1986). This measure of similarity provides results consistent with other common expressions [e.g., Jaccard's coefficient (Christiansen *et al.* 1990)], which give equal weight to all species and therefore tend to place excessive significance on rare species (Southwood 1978). In our study, rare species are conceptually very important, so overemphasizing their contribution to the community was not considered a serious shortcoming. Some coefficients of similarity take relative abundance into consideration (e.g., Bray and Curtis 1957), but these approaches have other shortcomings (Austin and Orloci 1966).

To understand how the entire community structure of the burned and unburned habitats differed, where possible, we classified the Hymenoptera into trophic categories based on the lowest taxonomic level of identification (Borror *et al.* 1989). Clearly, there are exceptions to these general categories, but this approach was consistently applied across all samples and allowed us to make reasonable inferences about trophic structure in the community, including those elements that were not directly sampled (e.g., plants, non-hymenopteran herbivores, fungivores, etc.). Because the missing samples were balanced between burned and unburned samples and represented similar times of year, we were able to validly pool the available data across dates and sites to avoid the problem of low sample sizes in generating an overall expression of community structure in burned and unburned habitats. Analysis of trophic associations in burned

and unburned habitats was performed using chi-square tests (Siegel 1956).

RESULTS

The Malaise trap samples yielded a total of 2,331 hymenopteran specimens, representing 603 species (morphospecies) from 36 families (Table 1). The majority of the species were Ichneumonoidea (60%); Chalcidoidea comprised 16% of the species, and Proctotrupeoidea made up 9% of the species. The aculeate Hymenoptera comprised only 10% of the species.

Species diversity increased sharply from early June through July and then gradually increased until September in all sites (Fig. 1). The sharp drop in diversity across all sites on the second sampling date was associated with an unusual cold front that caused snow at both sampling sites. The values and dynamics of species diversity in burned and unburned habitats were remarkably similar between sites. At both sites, the species diversity in burned habitats was generally lower than in unburned habitats throughout the summer, although the indices converged in late August or September. Diversity did not differ significantly ($F \leq 1.02$, $P > 0.30$) between burned and unburned sites in spring or late summer, but diversity was significantly ($F = 5.68$, $P = 0.07$) greater in unburned habitats in early summer.

The changes in species diversity appear to have been largely a function of species richness (Figs. 2). As with the trends in diversity, the number of hymenopteran species was significantly ($F = 7.74$, $P = 0.05$) greater in unburned habitats in early summer, with no significant ($F \leq 0.52$, $P \geq 0.50$) differences in other time periods. Richness generally increased throughout the summer. At site 1, the number of species in the unburned habitat increased rapidly in the first 6 wk of the survey, while the species richness in the burned habitat increased most rapidly later in the summer. At site 2, species richness increased at a relatively constant rate in both

Table 1. Species richness of Hymenoptera from Yellowstone National Park, 2 yr after the 1988 fires (taxa are arranged in descending order of species richness)

Taxon	Number of species	
Apocrita	596	
Ichneumonoidea	362	
Ichneumonidae		253
Braconidae		109
Chalcidoidea	96	
Pteromalidae		40
Torymidae		14
Eulophidae		11
Encyrtidae		8
Mymaridae		7
Eupelmidae		6
Eurytomidae		3
Eucharitidae		1
Perilampidae		1
Trichogrammatidae		1
unidentified		5
Proctotrupeoidea	55	
Diapriidae		46
Proctotrupidae		5
Platygastriidae		2
Scelionidae		2
Sphecoidea	19	
Sphecidae		19
Apoidea	18	
Halictidae		9
Anthophoridae		3
Megachilidae		3
Apidae		2
Andrenidae		1
Formicoidea	16	
Formicidae		16
Cynipoidea	14	
Cynipidae		1
unidentified		13
Chrysoidea	6	
Chrysididae		3
Dryinidae		2
Bethyloidea		1
Ceraphronoidea	5	
Megaspilidae		3
Ceraphronidae		2
Pompiloidea	2	
Pompilidae		2
Vespoidea	2	
Vespidae		2
Tiphioidea	1	
Tiphidae		1
Symphyla	7	
Tenthredinoidea	4	
Tenthredinidae		3
Argidae		1
Siricoidea	2	
Siricidae		2
Megalodontoidea	1	
Xyelidae		1

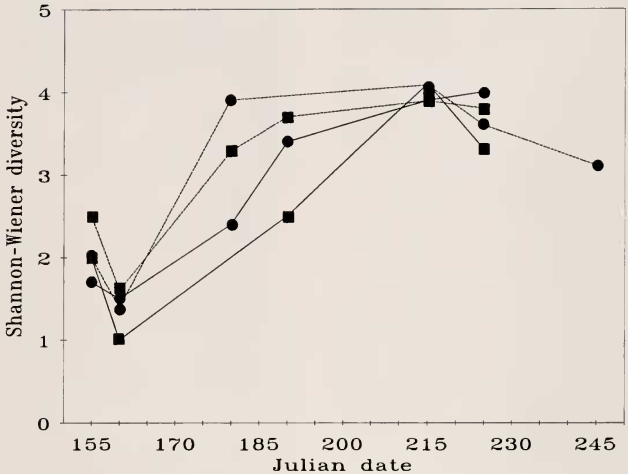


Fig. 1. Shannon-Wiener diversity in unburned (dashed line) and burned (solid line) habitats, at the southern (circles) and northern (squares) sample sites, 2 yr after the fires in YNP (Julian date 155 = 4 June; 185 = 4 July; 215 = 3 August; 245 = 2 September).

unburned and burned habitats after June. At the end of the summer, the number of species declined in all locations except the burned habitat at site 1. At both sites, more species were found in unburned habitats than in burned habitats throughout July and August. The unburned habitats peaked at 107 and 113 species, while the corresponding burned habitats had maxima of 88 and 90 species.

Species evenness was generally higher in unburned habitat than in burned habitats (Figs. 3). Indeed, unburned habitats had significantly greater ($F = 7.71$, $P = 0.03$) evenness than did burned sites during the spring, but no significant differences were found during the summer ($F \leq 0.25$, $P \geq 0.72$). Except for one sample from the burned habitat at site 1, species

evenness was greater than 80% in all samples. There was a general trend of decreasing species evenness in unburned habitats across the summer, but there was no discernible trend of evenness in burned habitats.

The hymenopteran communities from burned and unburned habitats at both sites were 0 to 20% similar across the summer (Fig. 4). Community similarity of burned and unburned habitats ranged from 0 to 14% at site 1, with a general trend towards increasing similarity with time. At site 2, community similarity ranged from 16 to 20%, with no discernible trend during the summer. The hymenopteran community similarities from the two burned habitats ranged from 5 to 30% throughout the summer. At only one

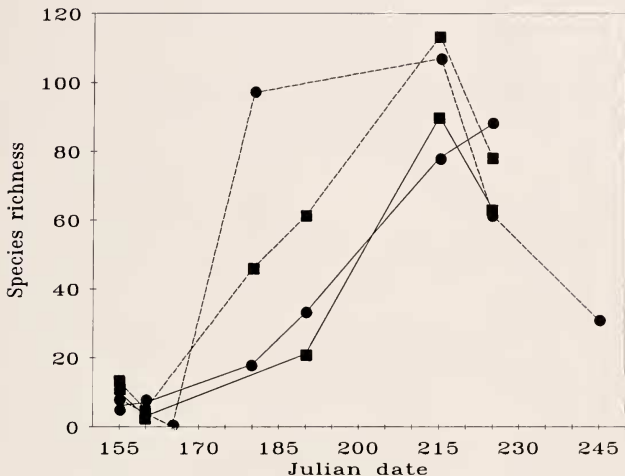


Fig. 2. Species richness in unburned (dashed line) and burned (solid line) habitats, at the southern (circles) and northern (squares) sample sites, 2 yr after the fires in YNP (Julian date 155 = 4 June; 185 = 4 July; 215 = 3 August; 245 = 2 September).

time was community similarity of the two burned habitats less than that found between the burned and unburned habitats within a site.

The community similarity between the two unburned habitats was consistently lower than between the burned habitats. The unburned habitats had community similarities ranging from 0 to 30%, with higher similarities later in the season. Thus, the similarity between hymenopteran communities in widely separated, burned habitats was greater than that found either between burned and unburned habitats at a single site or between widely separated, unburned habitats.

Analysis of trophic associations in burned and unburned habitats revealed significant differences in community

structure ($X^2 = 298.4$, 8 df, $P < 0.0001$; Table 2). In burned habitats parasitoid groups associated with herbivores on or in foliage but not in wood (e.g., Dryinidae, Microgastrinae, Hormiinae, and platygasterids) were significantly more frequent than in unburned habitats ($X^2 = 118.4$, 1 df, $P < 0.0001$). The domination of this trophic group in burned habitats (71% of the hymenopteran fauna) indicated that various grasses and forbs were providing the primary food source. This hypothesis is further substantiated by the significantly higher frequency ($X^2 = 24.8$, 1 df, $P < 0.0001$) of nectar-feeding Hymenoptera in these habitats as well. The herbivores of nonwoody plants and nectar-feeding species comprised only 52% of the hymenopteran community in unburned habitats. In

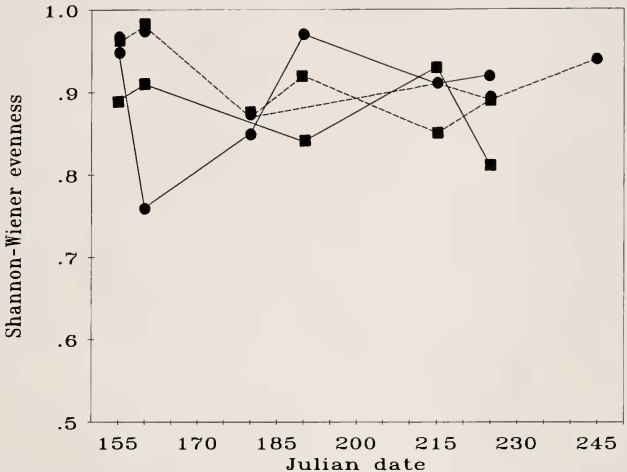


Fig. 3. Shannon-Wiener evenness in unburned (dashed line) and burned (solid line) habitats, at the southern (circles) and northern (squares) sample sites, 2 yr after the fires in YNP (Julian date 155 = 4 June; 185 = 4 July; 215 = 3 August; 245 = 2 September).

burned habitats, woody herbivores (i.e., Siricidae) and parasitoids of woody herbivores (e.g., *Dolichomitus imperator* (Kriechbaumer), *Rhyssa alaskensis* (Ashmead), *Triaspis pissodis* Viereck, *Allodorus crassigaster* (Provancher), and *Odontocolon* sp.) were significantly more frequent ($X^2 = 43.6$, 1 df, $P < 0.0001$) than in unburned habitats, where these trophic associations comprised only 1% of the Hymenoptera. In unburned habitats, parasitoids of fungivores and detritivores (e.g., Diapriidae, Proctotrupidae, Megaspilidae, and Cera-phronidae) were significantly more frequent than in burned habitats ($X^2 = 200.0$, 1 df, $P < 0.0001$). Being the most common trophic association (32%), these parasitoids indicated the importance of forest litter as a food source. These organisms

were infrequently found in burned habitats (9%), suggesting that the litter community and decompositional processes may have been adversely affected by fire.

DISCUSSION

The results of our surveys of hymenopteran species diversity in YNP 2 yr after the fires allow us the first opportunity to address empirically the central issues related to the effects of the fires on terrestrial biodiversity. Our findings 2 yr after the fires are particularly relevant to ecological and management discussions of short-term recovery in YNP (Lewin 1988, Romme and Despain 1989, McEneaney *in* Carr 1990, Skinner 1990, Varley *in* Jeffery 1990). In this context, we believe that the consistency of the data between these sites, the

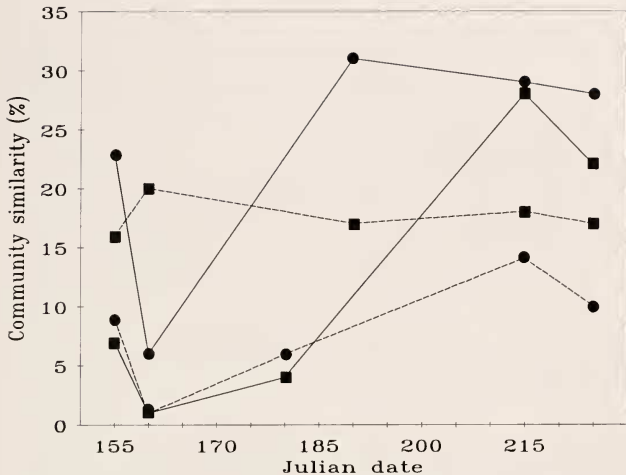


Fig. 4. Community similarity of burned habitats (solid line with circles), unburned habitats (solid line with squares), and burned and unburned habitats within sites (dashed line, southern site = circles, northern site = squares), 2 yr after the fires in YNP (Julian date 155 = 4 June; 185 = 4 July; 215 = 3 August).

quality of the taxonomic data, and the ecological qualities of the indicator taxon allow us to draw some reasonable inferences with respect to the effects of the fire on biodiversity. As previously noted, although Malaise traps, and all other collecting devices, are biased in the groups that they collect, the application of diversity indices to the data is appropriate as long as the interpretation of the analyses is developed in the context of the constraints of the sampling methodology (Southwood 1978). In this light, we can begin to address the three central questions raised previously.

Has biodiversity increased since the fires?—

Although we do not know what the status of biodiversity was immediately following the fires, we can reasonably infer that few

exposed insect populations survived the severe burns. As such, it would appear that a great number of species have recolonized burned habitats. Indeed, the species diversity and species richness in these habitats reached about 80% of presumed pre-fire levels within 2 yr. Thus, it is evident that substantial recovery of biodiversity has occurred since the fires.

The rapid recovery of biodiversity is not a function of an impoverished insect fauna prior to the fires. The notion that mature lodgepole pine forests are biological deserts (Romme and Despain 1989) is clearly erroneous. The diversity and richness of Hymenoptera in the unburned habitats was 5- to 10-fold greater than that reported for sagebrush habitats in Wyoming (Christiansen *et al.* 1990). If we assume

Table 2. Trophic associations of Hymenoptera collected from burned and unburned habitats of Yellowstone National Park, 2 yr after the 1988 fires

Trophic association (representatives)	Percent of sample from habitat (n, individuals)	
	unburned	burned
parasitoid of herbivores on or in foliage (most ichneumonids and braconids)	51 (750)	71 (844)
parasitoid of herbivores in wood (doryctine and helconine braconids)	1 (21)	6 (73)
parasitoid of detritivores, fungivores, and other litter associates (diapriids, proctotrupids, orthocentrine ichneumonids, alysiine and opiine braconids)	32 (464)	9 (104)
nest provisioning predator (sphecids, pompilids, vespids, chrysidids)	3 (41)	3 (38)
herbivore on or in foliage (tenthredinids, argids, xyelids, eurytomids, cynipids)	1 (15)	1 (9)
herbivore in wood (siricids)	0 (1)	0 (2)
nectar-pollen feeder (apoids)	1 (12)	4 (42)
scavenger (formicids)	11 (157)	5 (60)
hyperparasitoid (mesochorine ichneumonids)	0 (5)	1 (9)

that Hymenoptera account for 20% of insect species richness based on North American estimates (Schaefer and Kosztarab 1991), then an old-growth lodgepole pine habitat is likely to include 500 to 1,000 insect species. Although the vegetation may appear to approach a monoculture in these habitats, it is evident that the insect communities are diverse and differ markedly between stands. Even if the 20% insect community similarity between old-growth habitats is somewhat underestimated (for a discussion of this issue, see *Are there species unique to burned or unburned habitats?*), the total insect diversity supported in YNP's mature lodgepole pine forests is almost certainly of the order of several thousands of species. In this context it is important to note that the early successional insect communities in spatially disjunct burned habitats were more similar to one another than the communities in unburned habitats. This finding suggests that early successional communities tend to be relatively homogeneous,

and insect communities diverge with forest recovery.

Earlier work has suggested that the greatest diversity of selected plant (herbs, shrubs, and trees) and selected vertebrate (birds and mammals) species is found in young (1 to 25 yr-old) lodgepole pine forests (Taylor 1969, 1973, 1974; Taylor and Barmore 1980). Unfortunately, the species diversity of vertebrates in the 5 yr following a fire was not measured by Taylor (1969, 1973, 1974). However, plant species richness 1 to 3 yr after a burn was 9 to 23% of the maximum, which occurred 25 years after a burn. Bird and mammal species richness 7 to 13 yr after a burn was 65 to 81% of the maximum richness, which also occurred 25 yr after a burn. Species diversity dropped to 46% of the maximum in forests 57 to 111 yr after a burn.

Our data demonstrate that insect (Hymenoptera) biodiversity may recover at a rate similar to that of the plant community. If we assume that the biodiversity of

Hymenoptera tracks that of plants which harbor insects, we would expect the species richness 3 yr after a burn to be 79% of the richness found in a 60- to 100-yr old forest habitat, and our data indicate an 80% recovery. This rate of recovery is also similar to that found for aquatic macroinvertebrates (Minshall *et al.* 1990). The unburned habitats in our study were in forests that were at least 60-yr old and probably more than 100-yr old given that less than 3% of YNP had burned since 1930 (Taylor 1974). Cores from trees 4.2 km north of the South Entrance to YNP were determined to be 161 years old (Taylor 1969).

It should be noted that the 80% recovery does not take into account spatial patterns of diversity. In particular, the communities within the two burned habitats were much more similar to one another than were the communities from the two unburned habitats. As such, there appeared to have been a net loss of biodiversity across sites that was not reflected between habitats within sites.

The general similarities in the rate and pattern of biodiversity following the 1988 fires in the context of Taylor's (1969) research are somewhat surprising given that earlier conclusions were drawn from relatively species-poor groups and small-scale fires. There have been no previous attempts to measure biodiversity with insects, and the greatest recorded species richness of a forest habitat (using herbs, shrubs, trees, birds, and mammals combined over a 2 yr period) was 112 (Taylor 1973), which is one less than the number of hymenopteran species caught in a single trap over a 2-wk period (site 2, unburned habitat, July 14 to August 11). Given this finding and the relative rate of catch per unit effort for various taxa, there is little question that insects are superior indicators of biodiversity with respect to both information value and sampling efficiency (Hawksworth and Ritchie 1993).

We also might have expected differ-

ences between our biodiversity measures and those of Taylor (1969, 1973) due to the intensity of the 1988 fires relative to those studied in previous research. Indeed the total area burned by all fires in the YNP from 1930 to 1970 (24,030 ha) is just 6% of the area burned in 1988. However, it should be noted that our samples were taken within 500 m of the edge of the burned sites; sampling closer to the center of the major burns may well have revealed fewer species and slower recovery rates.

Are there species unique to burned or unburned habitats?—To address this question, we must first provide an interpretive context for the community measures derived from our study. It is clear that our sampling did not constitute a complete census of the hymenopteran community, so some species were undoubtedly missed in the course of our study. Although measures of endemism are sensitive to sampling intensity (i.e., incomplete sampling may artificially increase the apparent frequency of rare species, thereby reducing community similarity), in our study community similarity did not closely track sample size, suggesting that the frequencies of rare species across time and space were not an artifact of sampling intensity. Moreover, even if a habitat has a high frequency of apparently rare species by virtue of a sampling regime, this bias should be constant across sites so relative differences within our study are informative. Nonetheless, most measures of community similarity overemphasize the importance of rare species (Southwood 1978). Placing relatively greater weight on rare species is only problematical where emphasizing these taxa is undesirable, as may be the case in some ecological studies but not particularly in the context of biodiversity management and conservation in YNP. In light of these issues we can consider whether some species were unique to particular habitats and what this might mean in the context of conservation and management.

The fires evidently reduced hymenopteran diversity primarily through the loss of species (as opposed to decreasing species evenness). The low community similarities between burned and unburned habitats indicated that some species had not recolonized impacted areas in the 2 yr following the fires. In addition, some extraordinarily rare species were found in unburned habitats, including *Loxocephalus boops* (Wesmael), a euphorine braconid, presumed to be a parasitoid of adult ants and one of the rarest (or least often collected) braconids in North America. Given the occurrence of rare species and the low community similarities between unburned habitats at different sites, it appears that there is considerable habitat-level endemism among insect communities in lodgepole pine forests. Considering these factors in light of the scale of the 1988 fires, it is likely that species were locally extirpated, and it is possible that some species were extirpated from the Park. However, true extinctions are unlikely (Schullery 1989, Christensen *et al.* 1989, Skinner 1990), as there is no direct evidence that any hymenopteran species were endemic to our trap sites or YNP. Thus, without pre-fire surveys and more complete surveys of the insect fauna the actual loss of species from YNP can not be ascertained (Minshall *et al.* 1989).

Our measures of community similarity also provide some insight with regard to the dynamics which underlie the apparent habitat-level endemism in YNP. The low similarity between burned and unburned habitats at each site suggests that the post-fire hymenopteran fauna included species that were rarely or never collected in mature forests. These species were presumably exploiting hosts that were also rare in unburned habitats. In particular, the wasp fauna of burned sites was dominated by parasitoid species attacking larvae of Lepidoptera and Diptera. This provides a sharp contrast from the 1989 data (Lavigne *et al.* 1991), in which about 90% of the

hymenopterans sampled were aculeates (bees and predatory wasps). These results may indicate that large, strong-flying, flower-foraging hymenopterans were the first to migrate into the burned areas during 1989, and the insect host populations in burned areas may not have initially been sufficient to support many parasitoids. Thus, it appears that the new growth of grasses and forbs following the fires supported a herbivore community that differed markedly from that found in a mature forest. These unique, early-successional insect faunas were relatively homogeneous between burned habitats, but the communities reached a rather high level of biodiversity (80% of the species diversity and 70% of the species richness found in unburned sites) within 2 yr of the fire. It should be noted that the dramatic change in parasitoid populations may also be due, in part, to differences in the sampling methods from 1989 to 1990. Sweep sampling, although done periodically in 1989, favors collection from low vegetation (especially flowers) and consequently tends to selectively sample greater numbers of aculeates. Malaise traps, used in 1990, continuously sample flight activity and consequently capture many more minute forms, widely dispersing individuals, and crepuscular or nocturnal species.

In light of our findings and the challenges of interpretation, a thorough survey, perhaps even an All Taxon Biological Inventory (Yoon 1993, Janzen 1994), must be conducted in YNP if sound conservation policies are to be developed. Although this recommendation was first made 25 yr ago (Taylor 1969) it has not been heeded, and the management and conservation of biodiversity YNP and other ecological preserves continues to be handicapped as a consequence (Janzen 1994). The imminent need for such a survey is clearly demonstrated by our work, which included the collection of 46 species of Diapriidae, a family that was previously known to include only three species in

Wyoming, with no records from YNP (Lavigne and Tepidino 1976).

Have there been outbreaks of fire-adapted species?—Although we can not assert a direct, proportionate relationship (i.e., interval or ratio level of measurement) between host and parasitoid abundance, it is obvious that these variables are related at the nominal level of measurement and interpretations at the ordinal level are certainly valid (Siegel 1956). That is, to the extent that density-dependent relationships occur commonly (Hassell *et al.* 1989), but not invariably (Stiling 1987), in the Hymenoptera, more frequent occurrences of parasitoids can be interpreted as an indication of relatively greater host abundance. In this regard, the high levels of species evenness throughout this study suggest that there was not a numerically dominant hymenopteran species. If any life history could be considered dominant, it would appear that the majority of the parasitic Hymenoptera were probably attacking leaf-feeding, lepidopteran hosts in newly regenerating meadows. Anecdotal reports of tremendous ant biomass (McEaney *in Carr* 1990) and wood wasp outbreaks (Skinner 1990) in burned areas were not substantiated, although Malaise traps are not the most effective method for sampling either of these insect taxa. Ant abundance was substantially reduced in burned habitats. Only three wood wasps were found in our samples, and aggregations of wood wasps, when they occur, are probably very localized phenomena. Contrary to the assertions of Skinner (1990) it is not likely that these insects are a very regular, or significant, contribution to the diet of bears. In fact, our results indicate that wood wasp populations, along with other insects associated with decaying wood, are not dramatically enhanced by the fires.

Relatively few hymenopteran species in our samples were associated with wood or arbivorous hosts. Furthermore, it appears that there were no ongoing outbreaks of

host species of hymenopteran parasitoids at the burned sites. We found relatively few parasitoids of wood-boring beetles or arboreal Lepidoptera. Given that the major forest outbreak coleopterans and lepidopterans have associated hymenopteran parasitoids, it would seem that the forecasted outbreaks of bark beetle and other pests have not materialized (Knight and Wallace 1989). Knight and Wallace (1989) also noted the possibility that insectivorous birds had the potential to keep an impending outbreak in check (Taylor and Barmore 1980, Knight and Wallace 1989). Although slightly higher frequencies of ar-bivores and their parasitoids were found in burned sites, the dead wood did not provide the basis for a dramatic expansion of these trophic groups. Rather, the burned communities were typified by a marked increase in parasitoids of non-woody herbivores and nectar-feeders (indicating a flush of grass and forb growth) and a significant loss of parasitoids of fungivores and detritivores (indicating a loss of litter). It is likely that in the burned areas, much of the dead wood suitable for insect feeding was burned in the fires, and the severely charred trees were of little use to Hymenoptera or their hosts, except as nesting sites for some aculeates (ants, sphecids wasps, and bees). Thus, leaf cutter bees, which were found only in the burned habitats, may serve as a good indicator of the ecological conditions, as these insects depend on available nectar sources, broad-leaved plants, and nesting cavities.

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